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Agroforestry enables high efficiency of light capture, photosynthesis and dry matter production in a semi-arid climate

Dongsheng Zhang[a,1], Guijuan Du[b,1], Zhanxiang Sun[b,*], Wei Bai[b], Qi Wang[a], Liangshan Feng[b], Jiaming Zheng[b], Zhe Zhang[b], Yang Liu[b], Shu Yang[b], Ning Yang[b], Chen Feng[b], Qian Cai[b], Jochem B. Evers[c], Wopke van der Werf[c], Lizhen Zhang[a,*]

[a] College of Resources and Environmental Sciences, China Agricultural University, Beijing, 100193, China
[b] Tillage and Cultivation Research Institute, Liaoning Academy of Agricultural Sciences, Shenyang, 110161, Liaoning, China
[c] Centre for Crop Systems Analysis (CSA), Wageningen University, Droevendaalsesteeg 1, 6708 PB, Wageningen, The Netherlands

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ABSTRACT

Agroforestry systems, which combine annual crops with trees, are used widely in semi-arid regions to reduce wind erosion and improve resource (e.g. water) use efficiency. Limited knowledge is available on optimizing such systems by the choice of crop species with specific physiological traits (i.e. C3 vs C4, N-fixing vs non-N-fixing). In this study we quantified the light interception and utilization efficiency of trees and crops in agroforestry systems comprising apricot trees and a C3 species (sweet potato), a C4 species (millet) or an N-fixing legume species (peanut), and used measurements in the sole stands as a reference. A significant delay in leaf growth was found in millet. Maximum LAI of millet was 17% higher in agroforestry then expected from sole crop LAI, taking into account the relative density of 2/3, while a 25% decrease in maximum LAI compared to expected was observed in peanut and sweet potato. The total light interception in agroforestry was 54% higher than in sole tree stands and 23% higher than in sole crops. The millet intercepted more light and produced more biomass in agroforestry than peanut and sweet potato. The LUE values of the crops in the mixed systems were higher than those of the sole crops, as was the photosynthetic efficiency of individual leaves, especially in plants in the border rows of the crop strips. High light capture in agroforestry made a greater contribution to productivity of understory crops than the increases in light use efficiency. We conclude that agroforestry systems with apricot trees and annual crops, especially millet, can improve light utilization in semi-arid climates and contribute to regional sustainability and adaptation to climate change.

1. Introduction

Agroforestry (AF) has many benefits, including food production, biodiversity conservation (George et al., 2013), soil enrichment (Udawatta et al., 2008), carbon sequestration (Nair et al., 2009) and efficient resource use (Munz et al., 2014). It also plays an important role for a multifunctional and sustainable agriculture landscape (Schroth and da Mota, 2013) by offering ecological services and environmental benefits by reducing soil wind erosion and desertification (Branca et al., 2013). For these reasons, apricot-based agroforestry has been widely practiced in the Khorchin region in Northeast of China. The yield and water use efficiency of apricot agroforestry with annual crops millet, peanut and sweet potato were higher than sole stands, especially when a legume crop (peanut) or a C4 crop (millet) was used (Bai et al., 2016).

The overyielding of intercropping might be the result of an increase in light interception (Marshall and Willey, 1983; Du et al., 2015; Wang et al., 2015), light use efficiency (Gao et al., 2010) or a combination of both (Ceotto et al., 2013). Light interception (LI) is mainly determined by leaf area index and light extinction coefficient and might be affected by intercropping due to spatial configuration and changes in morphological traits of species (Zhang et al., 2014; Wang et al., 2016). Light interception of cotton in a jujube/cotton agroforestry decreased but light use efficiency increased (Zhang et al., 2014) due to the shading by the trees in agroforestry, which depends on the distance between the crop rows and the trees.

The light use efficiency (LUE) is defined as the efficiency of conversion of light into biomass, and is obtained from the slope of the linear relation between biomass and cumulative intercepted

* Corresponding authors.
E-mail addresses: sunzhanxiang@sohu.com (Z. Sun), zhanglizhen@cau.edu.cn (L. Zhang).
[1] These authors contributed equally to this work.

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photosynthetic active radiation (PAR) (Monteith, 1977; Sinclair and Muchow, 1999). LUE differs between C3 and C4 species and is affected by environmental and management factors such as the proportion of diffuse radiation (Dengel et al., 2015), temperature (Garcia et al., 1988), vapor pressure deficit (Gonias et al., 2012), nitrogen status (Garcia et al., 1988), water stress (Collino et al., 2001) and use of plant growth regulator (Mao et al., 2014). Crop LUE is higher in diffuse radiation than in direct light (Alton et al., 2007; Sinclair and Muchow, 1999). Water stress in crops reduces stomatal conductance, leading to a decline of internal CO_2 availability and thereby reduced photosynthesis and LUE (Zhou et al., 2016). LUE is determined mainly by crop net photosynthesis and is related closely to the leaf N concentration (Lawlor and Young, 1989). In agroforestry, trees remove a large fraction of the available light for the crops, and there is competition for water and nitrogen between trees and crops. Therefore, LI and LUE of crops in agroforestry likely depend on species traits such as C3 vs C4, and the ability to fix N: C4 plants can keep a higher carbon assimilation rate when in high light intensity or temperature, and N-fixing legumes in crop mixture systems can improve nitrogen uptake. However, important system characteristics remain unknown: does a C4 crop species show higher light use efficiency in agroforestry than C3? Does a legume in agroforestry improve LUE due to improved N-uptake?

An agroforestry canopy is temporally and spatially heterogeneous. To determine LI and LUE of shaded crops, it is essential but difficult to calculate the proportionsof radiation intercepted by the understory crop on a daily basis (Yang et al., 2014; Munz et al., 2014). A simple row structured crop model for light interception in strip intercropping (Pronk et al., 2003; Zhang et al., 2008; Wang et al., 2015) was successfully applied in agroforestry by Zhang et al. (2014). In this paper, we applied row-structured light-interception model to quantify overall LUE during the crop growth season of each crop at field level, and supported this with the measurements of radiation conversion efficiency (photosynthetic efficiency).

The objectives of this study were therefore to: (1) quantify light interception and use efficiency of crops in an apricot-based agroforestry system in relation to crop traits (C4/C3 and N-fixation/none); (2) to compare the overall light use efficiency at field level with photosynthetic efficiency at individual organ level to better understand the shading effect on light utilization in crop/tree mixtures.

2. Materials and methods

2.1. Field experiments

The field experiments were conducted in 2012 and 2013 at Zhanggutai (42°43′N, 122°22′E), Liaoning, China. The altitude is 226.5 m. The 30 years averaged annual air temperature is 7.2 °C, relative humidity is 59% and wind speed is 3.7–4.6 m s^{-1}. The soil is an aeolian sandy soil with a bulk density of 1.45 g cm^{-3}, measured by cutting-ring method, pH of 6.21, organic matter of 6.58 g kg^{-1}, total soil nitrogen content of 0.48 g kg^{-1}, total phosphorus of 0.28 g kg^{-1}, and total potassium of 26.95 g kg^{-1}. The total rainfall during the crop growing season was 526 mm in 2012 and 456 mm in 2013. The daily maximum and minimum air temperatures precipitation and radiation estimated by measured sunshine hours (Zhou et al., 2005) during the crop growing season are given in Fig. 1.

The experiments comprised seven cropping systems, which were three intercropping systems: (1) apricot (*Prunus armeniaca*) and millet (*Setaria italica*); (2) apricot and peanut (*Arachis hypogaea* Linn); (3) apricot and sweet potato (*Ipomoea batatas*); and 4 monocultures (4) sole apricot; (5) sole millet; (6) sole peanut; and (7) sole sweet potato. The experimental plots for all agroforestry treatments were laid out as a randomized block design with 3 replicates, and all plots for sole crops were laid out as a randomized block designed with 3 replicates in another field which was 150 m away from the agroforestry plots. Every plot covered an area of 67.5 m^2 (15 in length × 4.5 in width).

The apricot trees were 12-year-old in 2012 and 13-year-old in 2013. Distance between two adjacent tree rows was 4.5 m, and trees distance in a row was 2 m. The apricot had an average had an average plant height of 3.3 m at the time of the experiments. Apricots were harvested on July 19 in 2012 and July 23 in 2013. After apricot harvest, the leaves of trees stay green until the time of first frost. Six rows of crops (peanut, millet or sweet potato) were planted between tree rows at a row spacing of 50 cm (Fig. 2). The distance between a tree row and the adjacent crop row was 1.0 m. The plant density was 45 plants m^{-2} for millet, 25 plants m^{-2} for peanut and 6 plants m^{-2} for sweet potato in sole crops. The homogenous plant densities of mixing crops over whole intercropping area were 0.67 times the densities in sole crops, because only 67% of land was used to grow understory crops in the agroforestry. All crops were sown on May 21 in 2012 and 2013. All crops were harvested on September 25 in 2012 and September 20 in 2013.

Cultivars were Longwangmao for Apricot, LG2008-31 for millet, Baisha-1016 for peanut and Mingshui-1 for sweet potato. All crop cultivars were supplied by the Liaoning Academy of Agricultural Sciences. All plots received 375 kg ha^{-1} compound fertilizer (containing N 15%, P_2O_5 15% and K_2O 15%) before sowing. No further fertilizers were applied in 2012 whilst 225 kg ha^{-1} of ureophil (N 46%) was applied on July 30, 2013. No rhizobacteria were inoculated but nodulation of peanut was observed in the experimental plots after visual evaluation. No irrigation was given in both experimental years.

2.2. Dry matter and leaf area measurements

To determine LUE, dry matter and leaf area index (LAI) of the understory crops were measured five times on June 26, July 16, August 5, August 25 and September 14 in 2012; and on June 25, July 15, July 30, August 26 and September 20 in 2013. All plants in a sub-sampling area covering 1 m length in each crop row (6 rows) in each plot were separately harvested per row at each sampling time. Each sub-sampling area was at least 2 m apart from previous sampling areas to avoid border effects. The samples were separated into stems, leaves and reproductive organs. After weighting the fresh biomass, plant samples were oven-dried at 105 °C for 30 min to kill the tissues and then at 80 °C for approximately 2 days to achieve a constant weight.

The leaf length and width of all leaves of each of the sampled plants in each row and plot were measured using a ruler at the time of measuring fresh biomass. AThe individual leaf area was computed as the product of leaf length, width and an empirical leaf shape factor of 0.68 for millet (Oosterom et al., 2002; Payne et al., 1991) and 0.5 for peanut and sweet potato, as determined by the field observations. The leaf area index (LAI) was calculated as the product of plant density (per unit area of the whole agroforestry system) with plant leaf area. Specific leaf areas (SLA, m^{-2} kg^{-1}) was calculated as the ratio of measured LAI to leaf dry matter for each plot, separately for agroforestry and sole crop plots.

The LAI of apricot was estimated by a hemispherical image analysis using gap light analyzer software (Liu et al., 2013; Zhang et al., 2014). The images were taken at each sampling time for biomass by a fisheye camera (Nikon Co. Japan). The LAI of trees in each plot was averaged from three photos taken from the placements of tree row, 1 m from the tree line and the middle between the tree rows.

2.3. Simulation of leaf growth

The the beta growth function (Yin et al., 2003) was used to describe the dynamics of leaf area in different intercropping systems.

$$L = L_{max}\left(1 + \frac{t_e - t}{t_e - t_m}\right)\left(\frac{t}{t_e}\right)^{\frac{t_e}{t_e - t_m}} \quad (1)$$

$$C_m = \frac{2t_e - t_m}{t_e(t_e - t_m)}\left(\frac{t_m}{t_e}\right)^{\frac{t_m}{t_e - t_m}} L_{max} \quad (2)$$

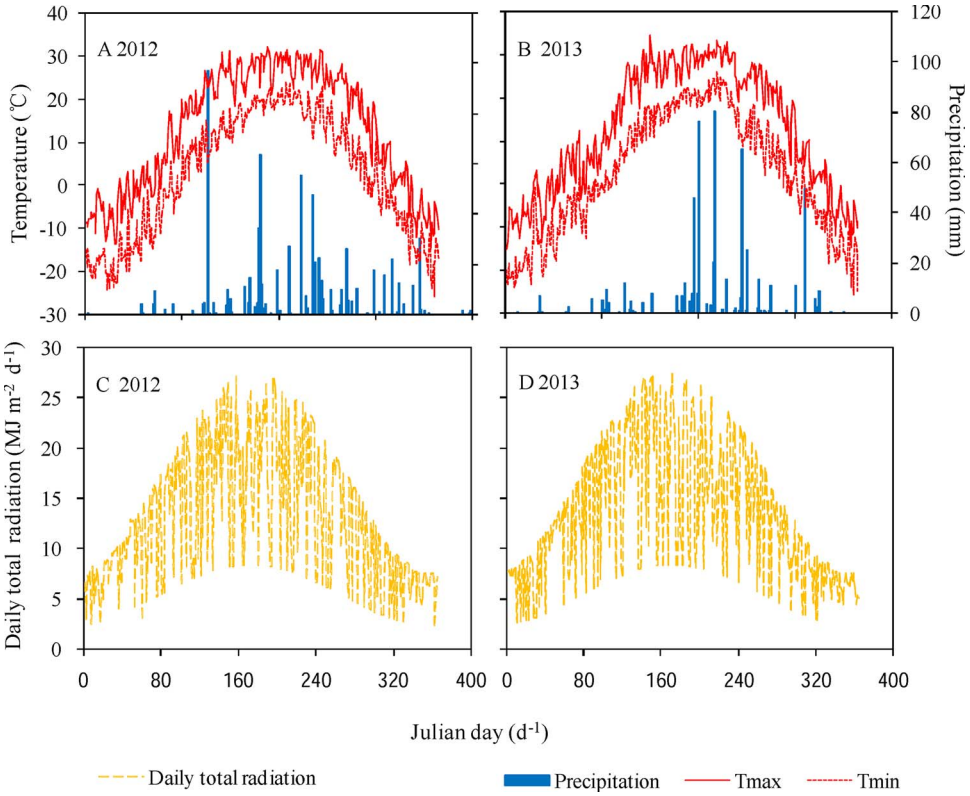

Fig. 1. Maximum and minimum air temperatures, precipitation and daily total radiation at Zhanggutai, Liaoning in 2012 (A and C) and 2013 (B and D).

Fig. 2. Experimental layouts of apricot/peanut (A) and apricot/millet (B) agroforestry in Liaoning, China.

where t_e (d) is the time reaching the maximum LAI value L_{max} ($m^2\,m^{-2}$), and t_m (d) is the time of reaching the maximal growth rate of leaf area C_m ($m^2\,m^{-2}\,d^{-1}$). The parameters of the equations were estimated separately for each plot. The results of replicates were used to conduct ANOVA.

2.4. Calculation of light interception and light use efficiency at field level

Daily light interception was calculated as the product of daily incoming PAR and the fraction of light interception. The accumulated light interception during the crop growing season was obtained by summing the daily values of light interception.

Daily incoming PAR was calculated on the basis of sunshine hours measured by a nearby weather station, using Angstrom's equation in a third-order form, expressed by:

$$\frac{H}{H_0} = w_1 + w_2\frac{S}{S_0} + w_3(\frac{S}{S_0})^2 + w_4(\frac{S}{S_0})^3 \quad (3)$$

where H is averaged daily global radiation, H_0 is the averaged daily extraterrestrial radiation, S is the actual sunshine duration, S_0 is the maximum possible sunshine duration, and w_1, w_2, w_3 and w_4 are empirical coefficients with values of 0.463, −0.893, 2.163 and −1.066, respectively, according to local conditions (Zhou et al., 2005).

The fraction of light interception of a component species i in the mixture ($f_{int,i}$) was computed using the row-structure crop model, based on measurements of leaf area index (L_i), plant height (h_i) and parameters describing geometry of the system such as strip width (w_i), path width (p_i) and canopy extinction coefficient (k_i) (Van Laar et al., 1997; Pronk et al., 2003). This model was previously improved and applied to simulate light interception successfully in wheat/cotton and wheat/maize intercropping systems (Zhang et al., 2008; Mao et al., 2014; Wang et al., 2015; Gou et al., 2017). In agroforestry, the simplifying assumption was made that the radiation transmitted between the tree rows is homogeneously distributed across the strips and then this model was used to estimate light interception in jujube/cotton agroforestry, the result of which was satisfactory when compared with measured light interception (Zhang et al., 2014).

2.4.1. The fraction of light interception for sole stands

$$f_{homo,i} = 1 - \exp(-k_i LAI_{homo,i}) \quad (4)$$

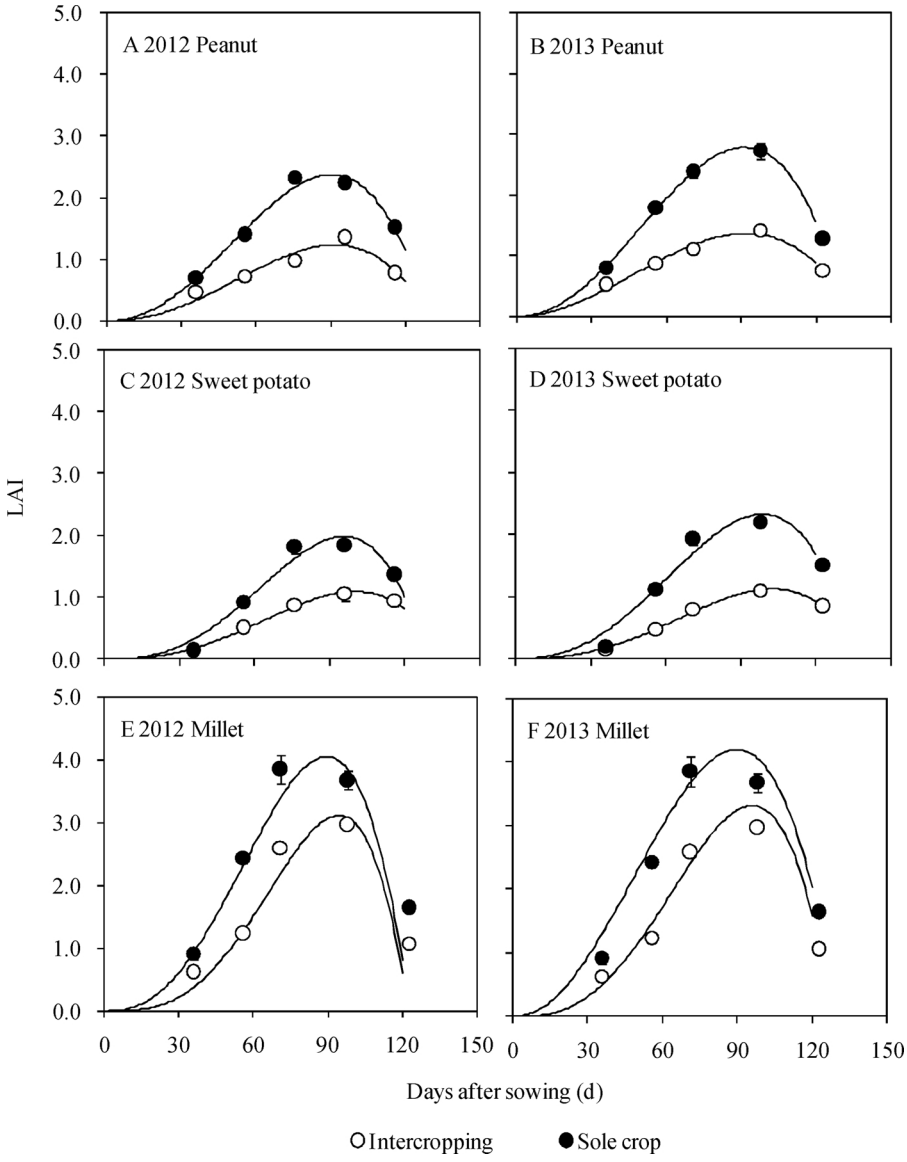

Fig. 3. Growth dynamics of leaf area index (LAI) of intercropped crops in agroforestry and sole stands in 2012 and 2013.

The light intercepted by a canopy of a sole stand, a homogeneous crop ($f_{\text{homo,i}}$), was described as an exponential extinction function of leaf area index ($LAI_{\text{homo,i}}$) and light extinction coefficient (k_i). The subscript i refers to the species (peanut, sweet potato, millet and apricot). The k_i represents the light extinction coefficient of crop i. $LAI_{\text{homo,i}}$ is the homogeneous leaf area index of crop i.

2.4.2. The fraction of light interception for intercropped crops

$$f_{int,i} = f_{homo,i} - \frac{S_{p,i} - S_{s,i}}{1 - \exp(-k_i LAI_{comp,i})}(f_{homo,i} - f_{comp,i}) \quad (5)$$

The light intercepted by understory crops ($f_{\text{int,i}}$) was calculated as a weighted average of light interception by a homogenous canopy ($f_{\text{homo,i}}$) and light interception by a fully compressed canopy ($f_{\text{comp,i}}$). The coefficient $f_{\text{comp,i}}$ is derived from Eqs. (6) and (7).

$$LAI_{comp,i} = LAI_{homo,i}\frac{w_i + p_i}{w_i} \quad (6)$$

$$f_{comp,i} = \frac{w_i}{w_i + p_i}(1 - \exp(-k_i LAI_{comp,i})) \quad (7)$$

where, w_{i} and p_{i} are widths of the crop strip and the path for apricot or intercropping crops.

In Eq. (5), the intermediate expression, $(S_{\text{p,i}} - S_{\text{s,i}})/(1 - \exp(-k_{\text{i}} LAI_{\text{comp,i}}))$, is a weight coefficient, where $S_{\text{p,i}}$ is the fraction of light transmitted to the soil surface in the path and determined by direct radiation (a_{i}) and radiation transmitted from neighboring crop rows ($(1 - a_{\text{i}})\exp(-k_{\text{i}} LAI_{\text{comp,i}})$).

$$S_{p,i} = a_i + (1 - a_i)\exp(-k_i LAI_{homo,i}) \quad (8)$$

$$a_i = \frac{\sqrt{h_i^2 + p_i^2} - h_i}{p_i} \quad (9)$$

where, a_{i} is a view factor over the path. It is the relative light reaching the path directly when the canopy is assumed as a black block, where light could only transmit to the path from the top with a view angle. h_{i} is plant height.

Similarly, $S_{\text{s,i}}$ refers to the relative light transmitted to the soil surface under the strips.

$$S_{s,i} = b_i \exp(-k_i LAI_{comp,i}) + (1 - b_i)\exp(-k_i LAI_i) \quad (10)$$

$$b_i = \frac{\sqrt{h_i^2 + w_i^2} - h_i}{w_i} \quad (11)$$

where b_i is a view factor over the strip.

Table 1
Fitted parameters for the growth of leaf area in intercropped crops in apricot-based agroforestry and in sole stands in 2012 and 2013.

Year	Crop	L_{max}		t_m		t_e		C_m		R^2	
		Intercrop	Sole	Intercrop	Sole	Intercrop	Sole	Intercrop	Sole		
		$m^2 m^{-2}$		d		d		$m^2 m^{-2} d^{-1}$			
2012	peanut	1.2 aA	2.4 bA	52 aA	50 aA	92 aA	90 aA	0.021 aA	0.041 bA	0.97	0.98
	sweet potato	1.1 aA	2.1 bA	64 aB	63 aC	100 aB	96 bB	0.023 aA	0.039 bA	0.96	0.94
	millet	3.1 aB	4.1 bB	66 aB	60 bB	94 aA	89 bA	0.057 aB	0.082 bB	0.97	0.96
	SE	0.278	0.265	1.942	1.546	1.204	0.939	0.006	0.005		
2013	peanut	1.4 aA	2.8 bA	47 aA	50 aA	92 aA	91 aA	0.018 aA	0.048bA	0.95	0.95
	sweet potato	1.1 aA	2.3 bA	66 aB	61 bB	103aC	98 bB	0.022 aA	0.042 bA	0.94	0.96
	millet	3.3 aB	4.2 bB	64 aB	56 bA	96 aB	89 bA	0.062 aB	0.071 aB	0.96	0.96
	SE	0.297	0.243	2.553	1.804	1.406	1.531	0.005	0.004		
Mean	peanut	1.3 aA	2.6 bA	50 aA	50 aA	92 aA	90 aA	0.024 aA	0.043 bA	–	–
	sweet potato	1.1 aA	2.2 bA	65 aB	61 bB	101aB	97 bB	0.023 aA	0.041 bA	–	–
	millet	3.2 aB	4.1 bB	65 aB	58 bA	95 aA	89 bA	0.061 aB	0.071 bB	–	–
	SE	0.286	0.253	2.187	1.589	1.251	1.147	0.005	0.004		
F	System	319[b]		33.8[b]		13.1[b]		181[b]			
	Year	9.78[b]		8.74[b]		2.49		0.06			
	Crop	420[b]		82.5[b]		27.1[b]		285[b]			
	System*year	1.49		0.29		0.001		2.78			
	System*crop	3.03		21.1[b]		2.03		2.45			
	Crop*year	0.44		2.43		0.44		3.72[a]			

Same small letters indicate no significance between intercropping and monoculture for the same crop and year at α = 0.05.
Same capital letters indicate no significance between crops species within the same year at α = 0.05.
[a] indicates a significant difference between at a 5% level.
[b] at a 1% level.

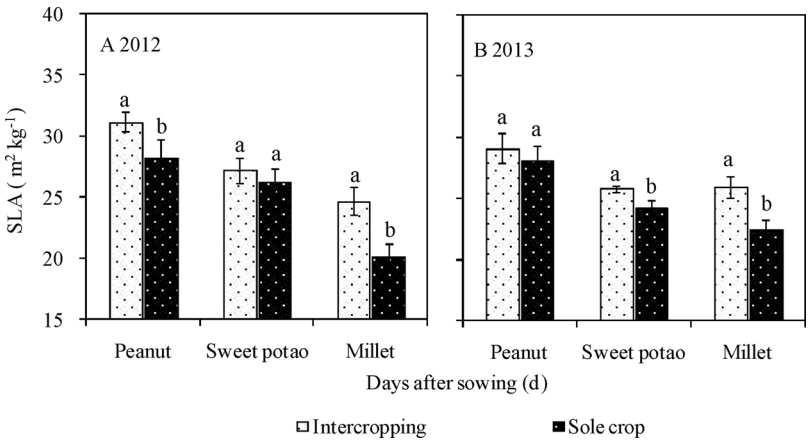

Fig. 4. Specific Leaf area (SLA) averaged during crop growing season for mixing crops in the agroforestry and in sole stands in 2012–2013.

For the tree in the agroforestry and sole stand, the fraction of light interception was calculated using Eq. (5). However, for understory crops, the incoming radiation reaching the top of their canopy had been reduced by a shading from tall trees and a strip compressed leaf area of mixing crops. So, a radiation reduction factor $S_{p,tree}$, calculated with Eq. (8), and a proportion of ground area occupied by mixing crops strips, $w_{crop}/(w_{crop} + p_{crop})$, were used to quantify the reduction of incoming radiation at the top of the shaded crops. The coefficient $f_{int,crop}$ in Eq. (5) is for the no shading situation. Therefore, the actual fraction of light interception by understory crops ($f_{int,actual,crop}$) was calculated by Eq. (12), where *i* refers to a shaded crop in the strip structured agroforestry.

$$f_{int,actual,crop} = \frac{w_{crop}}{w_{crop} + p_{crop}} S_{p,tree} f_{int,crop} \quad (12)$$

For crops in the agroforestry systems, the strip width of each understory crop (w_i) was 3.0 m (6 rows × 0.5 m row spacing), while the path width (p_i) (tree strip width) is 1.5 m according to the crown width of the trees. For trees, the strip width (w_i) was 1.5 m and the path width (p_i) was 3.0 m. The extinction coefficient of crops and tree in both agroforesry and monocultures was 0.6 for peanut (Awal et al., 2006), 0.67 for millet (Ong and Monteith, 1985), 0.8 for sweet potato (Nelson et al., 2005) and 0.95 for apricot. The crop heights input in the model were actually measured at the time of LAI measurements during growing seasons and tree height was measured once at end of a season. LAI used in the model was obtained from fitted sigmoid functions from field measurements for each plot.

Finally, the overall light use efficiency during the crop growth season was the slope of the linear regression between dry matter and accumulated light interception.

2.5. Measurements of leaf photosynthesis and photosynthetic efficiency at leaf level

Leaf photosynthesis rate was measured using a LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA) with a dot light quantum probe mounted onto a 6 cm^2 clamp-on leaf chamber. The measurements were conducted from 11:00 to 13:00 h on sunny days. Ten plants were selected randomly in each row per plot. First fully expanded top leaves of each plant (totally 10 top leaves for each row) were measured during the peak LAI period on June 4 in 2012 and June 6 in 2013 for peanuts, July 28 in 2012 and July 24 in 2013 for millet and June 26 in 2012 and June 23 in 2013 for sweet potato. The

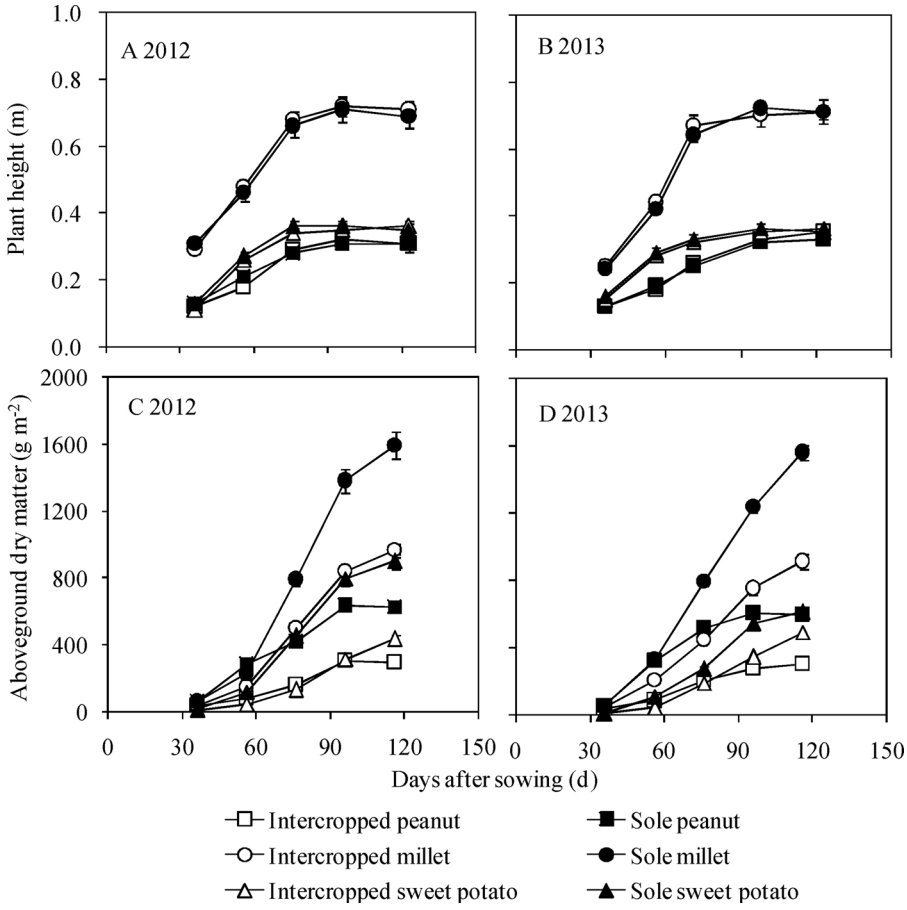

Fig. 5. Growth dynamics of the plant height and aboveground dry matter of mixing crops in agroforestry and sole stands in 2012 and 2013.

sampling rows in each plot were the first border row close to the tree line and the two middle rows of the crop strips. The photosynthetic parameters, i.e. ambient PAR intensity reaching the surface of measured leaves, net photosynthesis rate (Pn), stomatal conductance, transpiration rate and intercellular CO_2 concentration were recorded. The photosynthetic efficiency of individual leaves (ε, in *u*mol CO_2 *u*mol PAR^{-1}), was calculated as the ratio of the measured leaf net photosynthesis (Pn) to ambient PAR intensity at surface of measured leaves.

2.6. Statistical analysis

The statistical software SPSS 20 (IBM, USA) was applied for an analysis of variance (ANOVA). Least significant differences were used to separate means of crop dry matter, photosynthetic parameters and LUE among treatments at the 5% level. The significant differences between treatments were analyzed using the independent samples paired *t*-test at a level $\alpha = 0.05$ for parameters of sigmoid function for leaf area growth.

3. Results

3.1. LAI, specific leaf area, plant height and dry matter

The course of LAI over time fitted the beta function well, with a determination coefficient above 0.94 (Fig. 3 and Table 1). Considering the LAI expected in mixed crops was two thirds of that of sole crops, following the proportion of land area taken up by the crop, the actual maximal LAI (L_{max}) of intercropped millet was 16.5% in the agroforestry compared to the sole stand, while it was 25.4% lower than expected on the basis of sole crop LAI in intercropped peanut and sweet potato (Table 1). Maximum LAI growth rate (C_m) of millet was 28.2% higher than monoculture millet, but was 16.5% lower for intercropped peanut and sweet potato compared with the respective monocultures. The moment the maximal LAI (t_e) and maximal LAI growth rate (t_m) for millet was reached, was significantly delayed by 7 and 6 days in agroforestry compared to the monocultures, respectively, and by 4 days for both parameters for sweet potato, while no delay was observed for peanut. (Table 1 and Fig. 3). LAI of apricot was not different between intercropping and sole systems, with an average value of 2.79 ± 0.08 ($P > 0.05$). The specific leaf area (SLA) of understory crops in the agroforestry was higher than in sole crops (Fig. 4), especially for millet in which SLA significantly increased 18%.

Plant height of apricot trees and understory crops was not affected by the agroforestry (Fig. 5A and B). Based on the land proportion of the understory crops in the agroforestry, the actual dry matter of millet was 11% lower than expected from the sole crop dry matter. For peanut and sweet potato, it was 25% lower in the agroforestry than expected from the sole systems (Fig. 5C and D and Table 2).

3.2. Light interception

The total fraction of light interception of the agroforestry systems was higher than in the sole crops and tree, especially during the seedling stage of the crops (Fig. 6C and F). The fraction of light interception of apricot trees in agroforestry did not differ from the tree mono stands. The total cumulative light interception (trees + crops) in agroforestry, across all systems and both years, was 53.9% higher than in sole tree and 23.3% higher than in sole crops respectively (Fig. 7).

The relative plant density of the crops in the agroforestry systems was 67% of the sole system. Considering relative density of the mixed crops, the actual reduction in light capture was 30% in millet, 40% in peanut and 43% in sweet potato (Table 2 and Fig. 7) compared to sole

Table 2
The maximal aboveground dry matter (DMmax), cumulative light interception (LI) and LUE (g DM per MJ PAR interception) at field level and light-CO_2 conversion efficiency (ε, μmol CO_2 per μmol PAR) at leaf level in intercropped crops and sole stands in 2012 and 2013.

Year	Crop and system		DMmax g m^{-2}	△DMmax %	LI MJ m^{-2}	△LI %	LUE g MJ^{-1}	△LUE %	ε μmol μmol^{-1}	△ε %
2012	*Peanut:*	Intercrop	300 a	−28	194 a	−37	1.61 a	8	0.0142 a	4
		Sole	624 b		459 b		1.49 b		0.0136 a	
		SE	32.42		56.32		0.034		0.00082	
	Sweet potato:	Intercrop	433 a	−28	216 a	−42	1.92 a	12	0.0145 a	9
		Sole	898 b		560 b		1.71 b		0.0133 b	
		SE	41.38		86.74		0.051		0.00031	
	Millet:	Intercrop	963 a	−10	296 a	−29	2.79 a	25	0.0187 a	18
		Sole	1594 b		624 b		2.24 b		0.0158 b	
		SE	63.54		101.5		0.121		0.00072	
2013	*Peanut:*	Intercrop	307 a	−24	179 a	−43	1.69 a	20	0.0151 a	13
		Sole	600 b		468 b		1.41 b		0.0133 b	
		SE	19.25		67.54		0.041		0.00052	
	Sweet potato:	Intercrop	493 a	−19	171 a	−44	2.33a	23	0.0141 a	3
		Sole	912 b		458 b		1.89b		0.0136 a	
		SE	35.24		32.58		0.151		0.00037	
	Millet:	Intercrop	914a	−13	285 a	−31	2.89 a	27	0.0181 a	14
		Sole	1562 b		615 b		2.27 b		0.0159 b	
		SE	71.28		86.34		0.125		0.00078	
Mean	*Peanut:*	Intercrop	302 a	−26	187 a	−40	1.65 a	14	0.0147 a	9
		Sole	612 b		464 b		1.45 b		0.0135 b	
		SE	30.24		51.63		0.042		0.00054	
	Sweet potato:	Intercrop	463 a	−24	193 a	−43	2.13 a	18	0.0143 a	6
		Sole	905 b		509 b		1.80 b		0.0135 b	
		SE	36.52		48.61		0.124		0.00035	
	Millet:	Intercrop	939 a	−11	291 a	−30	2.84 a	26	0.0187 a	16
		Sole	1578 b		620 b		2.26 b		0.0159 b	
		SE	68.56		90.74		0.124		0.00072	

△DMmax is the relative difference between observed maximum dry matter of crops in the agroforestry and the expected dry matter, taking into account the proportion of ground area used by understory crops in the agroforestry (P_c, 0.67), and is calculated as $(DMmax_{intcrop} - Pc \times DMmax_{sole})/(P_c \times DMmax_{sole})$. Similarly, △LI is the relative difference between observed and expected maximum light interception, and is calculated as $(LI_{intcrop} - Pc \times LI_{sole})/(P_c \times LI_{sole})$. △LUE and △ε represent the percentage difference between observed LUE and ε between mixed and sole crops. The ε value is the average of the first border row and middle row. Same small letters indicate no significance between intercropping and monoculture at α = 0.05 for each crop and year.

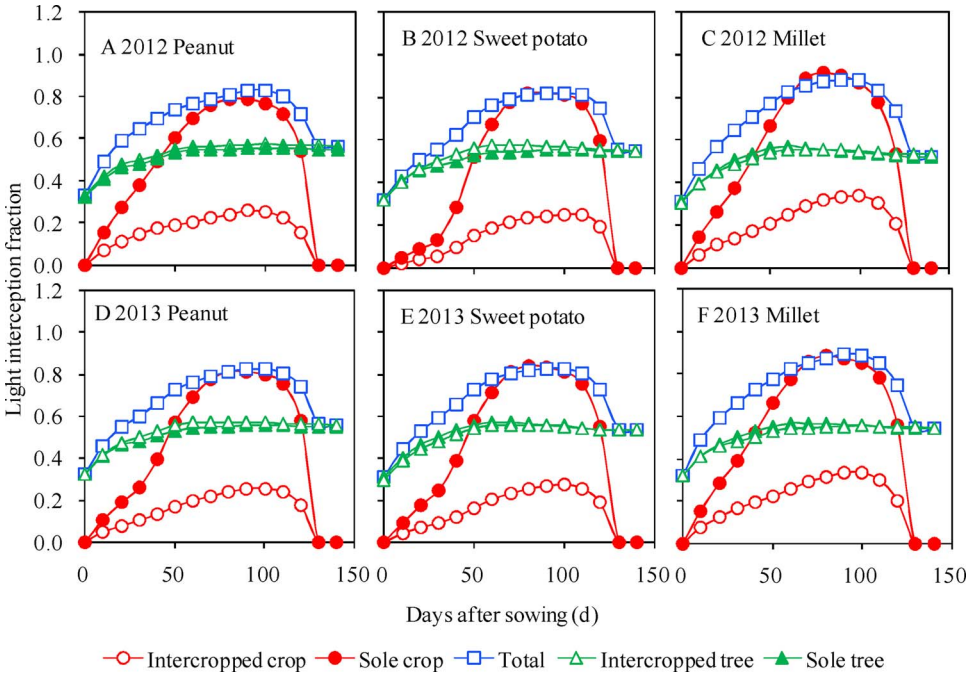

Fig. 6. Dynamics of light interception fraction in intercropped and sole tree and crops in 2012–2013.

crops. This reduction in light capture was partially due to the shading of trees and to the plasticity of crop growth, i.e. lower plant leaf area and higher SLA, in response to shading.

3.3. Light use efficiency at field level

Although crop biomass and light capture per m^2 of total area were lower in agroforestry than in monoculture in all crop species, the LUE, represented by the slope of the linear regression between dry matter and cumulative light interception ($R^2 > 0.93$ across two years), was

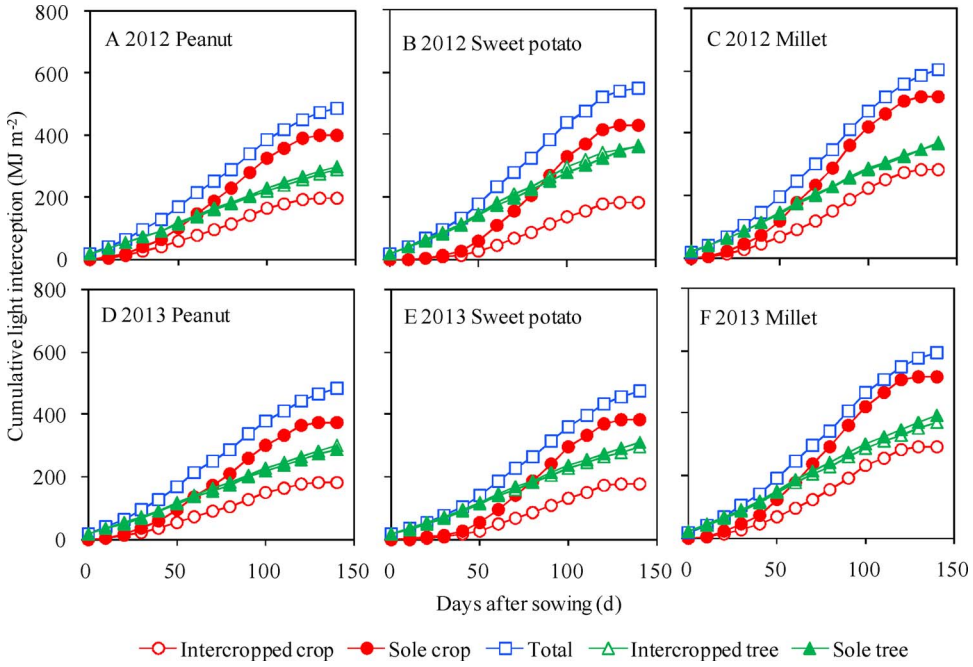

Fig. 7. Dynamics of cumulative light interception of mixing and sole tree and crops in the agroforestry and sole stands in 2012–2013.

14%, 18% and 26% higher in agroforestry than in monoculture for peanut, sweet potato and millet, respectively. LUE values were 1.65 g DM (MJ PAR)$^{-1}$ for peanut, 2.13 g DM (MJ PAR)$^{-1}$ for sweet potato and 2.84 g DM (MJ PAR)$^{-1}$ for millet (Table 2). Especially millet appeared to be very efficient in converting light into biomass when grown in agroforestry with apricot (Fig. 8 and Table 2).

3.4. Photosynthesis and photosynthetic efficiency at leaf level

Incident PAR intensity was 84% lower in the first border row close to tree lines than in the middle rows across all agroforestry systems and years. No difference in incident PAR was observed for any of the crop species between the middle rows in the AF systems and the monocultures (Fig. 9A and B). Average net photosynthesis rates (Pn) were 78% lower in leaves in border rows of crops in the AF systems than in middle rows (Fig. 9C and D). Pn of sweet potato, the C3 species, was significantly lower in middle rows than in the sole stand in 2013 but not in 2012. The peanut showed a significantly lower Pn in the middle rows than in the sole stand in 2012 but not in 2013. There was no significant difference in Pn of millet between middle rows in AF and sole stands in either year. The photosynthetic efficiencies at leaf level (ε) were higher in the border rows of understory species in the agroforestry than in the middle rows and the sole stands ($P < 0.05$) (Table 2). The ε of mixed peanut and sweet potato was lower in the middle rows of AF than in sole stand in both years, but the opposite (significantly higher ε) was found for millet in the middle rows of AF as compared to sole stand (Fig. 9E and F). There were no significant difference in ε between peanut (legume) and potato (non-legume) at any position in the AF or sole crop systems (sweet potato) (Table 2).

4. Discussion and conclusions

The total light interception in agroforestry was 54% higher than in the sole tree stand and 23% higher than in sole crops. The millet intercepted more light and produced more biomass than peanut and sweet potato. The LUEs of shaded crops in agroforestry were higher than in sole crops, which was associated with observation of higher photosynthetic efficiency of individual leaves in the intercrops, especially in border plants. The intercropped millet, as a C4 and drought tolerant species, showed a greater increase in light interception and LUE over monoculture than peanut and sweet potato. The higher LI and LUE in millet were related to a delay in leaf growth, caused by the tree shading. The maximum LAI of millet was 17% higher in the agroforestry than expected on the basis of the LAI in sole stands when the relative density of 2/3 was accounted for, while maximum LAI of peanut and sweet potato was 25% lower. As a result of the delay in canopy growth of crop species in the agroforestry crop development occurred during a period with higher incoming radiation. Therefore, even though the trees in the agroforestry removed part of this light, over the whole season the crop captured more light when grown in agroforestry. The C4 and drought tolerant millet showed the strongest improvement in crop light interception due to (1) a longer life span of leaves than sole crop, (2) thinner and larger leaves than the sole crop as a result of a significant increase of specific leaf area (SLA) in the AF, consistent with previous work in jujube/cotton agroforestry (Wang et al., 2016), and also (3) improved water uptake (Bai et al., 2016) as a result of deeper root distribution (Brück et al., 2003).

The improvement in LUE of mixed crops made only a small contribution to enhancing production of agroforestry. LUE for sole C3 species ranged from 1.41 to 1.89 g DM MJ (PAR)$^{-1}$ at field level, which was consistent with a wide range of previous studies with values from 1.35 to 3.0 g DM MJ (PAR)$^{-1}$ (Prince, 1991; Ruimy et al., 1994). LUE for C4 millet in sole system was 2.26 g DM MJ (PAR)$^{-1}$, which was also similar to previous study (2.0–2.5 g MJ^{-1}) (Squire and Monteith, 1984). LUE values of crops were higher in the agroforestry than in sole crops, consistent with results observed in jujube/cotton agroforestry (Zhang et al., 2014). This increase in LUE in agroforestry might be caused by: (1) the increase of diffuse radiation due to the shading from apricot trees (Stirling et al., 1990; Gu et al., 2002; Urban et al., 2007; Dengel and Grace, 2010; Dengel et al., 2015; Urban et al., 2012); (2) mitigating nitrogen competition by increasing nitrogen content of leaves (Lawlor and Young, 1989; Shah et al., 2004) due to a nitrogen fixation for leguminous plants (Fletcher et al., 2013); and (3) the improvement of water availability and use efficiency (Bai et al., 2016). Millet had a substantially greater increase in LUE in the agroforestry than the two C3 species. However, in contrast to our expectations, intercropping a legume in agroforestry did not result in a higher LUE than a non-legume.

Our study showed that the net photosynthetic efficiencies (ε) at leaf level in the mixed crops were significantly higher than in sole stands,

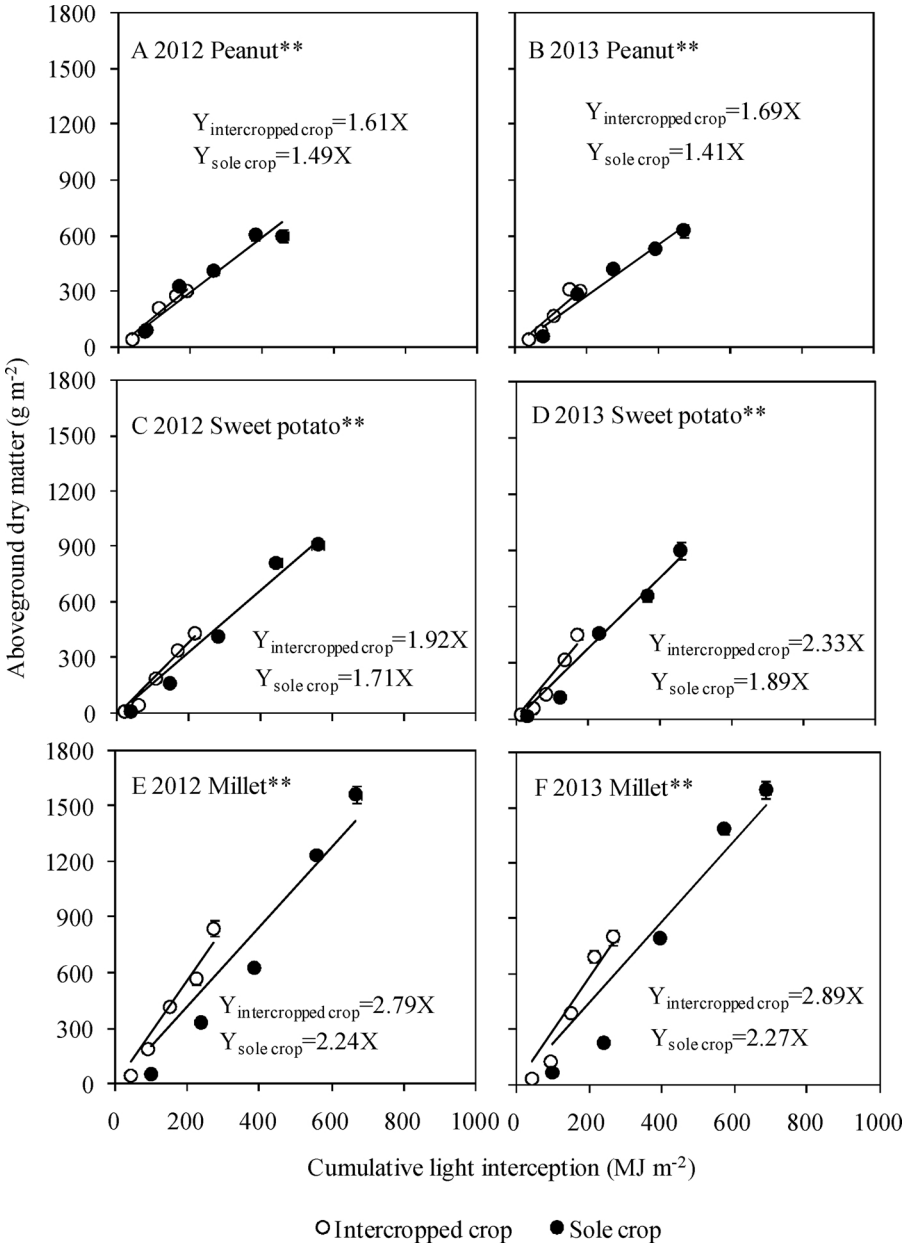

Fig. 8. Relationships between aboveground dry matter and light interception during crop growing season for three agroforestry systems and sole stands in 2012–2013. The slope of the regression line is the light use efficiency (LUE). ** indicates a significant difference of LUE between intercropped and sole crops at $\alpha = 0.01$ level.

especially in heavily shaded border rows. Because the photosynthesis measurements were conducted during a sunny day under optimal crop growth conditions (without or with minimal water and nitrogen stress), the increase of ε could be attributed mostly to the increase in the proportion of diffuse radiation due to tree shading. On average of three intercrops, the increase of photosynthetic efficiency $\triangle\varepsilon$ at leaf level was 53% of the overall increase of LUE at field level during growing season ($\triangle$LUE), indicating that the shading in agroforestry contributed around 50% to enhancing LUE and another 50% probably from belowground inter-specific interactions (Farquhar and Roderick, 2003; Mercado et al., 2009). Other likely contributors were complementarily use of water and nutrients (Bai et al., 2016) and an increased life span of leaves due to a developmental delay found in this study and higher SLA (Wang et al., 2016), both caused by plastic responses to the intercropping situation. The absence of any significant effect of legumes on improving LUE in the agroforestry might have been caused by an absence of N-limitation in our experiments, which might limit the extent and importance of N-fixation by peanut. However, the contribution of N-fixation by legume crops in intercropping to the increases of yield and light use efficiency requires further studies by comparing with no nitrogen control. To our knowledge, this is first report of evidence that relates photosynthesis and LUE estimates of crops to the extent of tree shading in agroforestry in relation to row position.

Choice of species combination, e.g. mixing drought tolerant crops with optimal root distribution (deep and big root system) and/or C4 species with higher light conversion efficiency (Willey and Reddy, 1981) may contribute substantially to enhanced land productivity in agroforestry, by increasing resource capture and use efficiency. Appropriate management to enhance the productivity of understory crops in agroforestry could also be pruning tree crowns (Hou et al., 2003), increasing distance between adjacent crop border row and tree line to minimize interspecific competition, or increasing plant density of mixing crops (Zhang et al., 2014, Mao et al., 2014, Wang et al., 2016).

It is very difficult to quantify light interception and use efficiency in intercropping is using field measurements because of the interaction between species in light capture. A model approach is currently the best way to explore light competition in intercropping. However, over- or under-estimations in light interception may occur, and models are

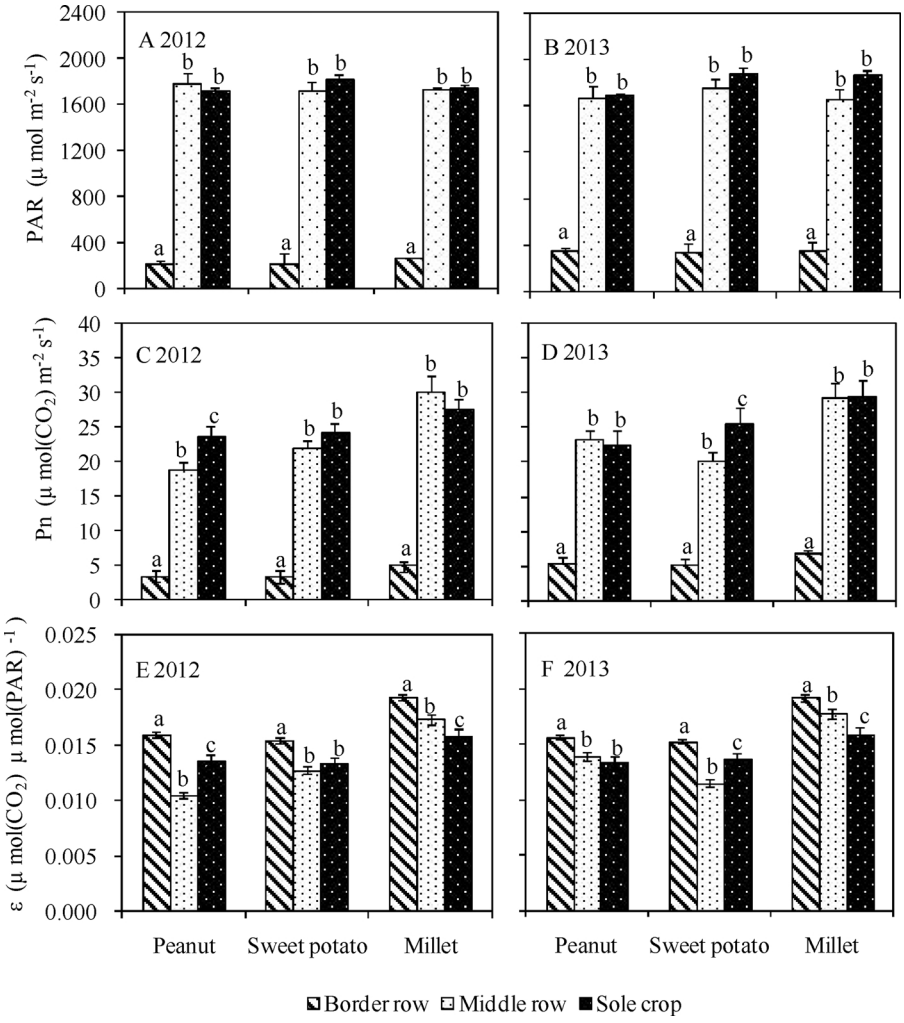

Fig. 9. Light intensity reaching leaves surface, net photosynthesis rate and light-CO_2 conversion efficiency (ε) at leaf level of understory crops in the agroforestry and in sole stands in 2012 and 2013. The same small letters indicates no difference between border row, middle row and sole stand for the same crop species.

difficult to validate experimentally because they give predictions of average light interception not taking into account the season and daily courses in the position of the sun and the state of the atmosphere, whereas measurements vary with time of day, time of the season, and fraction diffuse radiation. Further studies using functional-structural plant (FSP) models will help to directly quantify spatial light distribution and interception (Mao et al., 2015; Evers, 2016) in relation to the spatial row configuration, plant density, position of the sun, and the proportion of diffuse radiation in intercropping (Mao et al., 2016). FSP models could be also applied to validate the process-based intercropping model and to explore the effect of interspecific competition and complementarity, especially for light, in relation to plant functional and structural plasticity. In general, our results could help farmers to improve light utilization in semi-arid climate and can play an important role on regional sustainability and adaption to climate change, especially, for millet/apricot intercropping.

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